Familiarity-Based Stimulus Generalization of Conditioned Suppression.

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Abstract

We report that stimulus novelty/familiarity is able to modulate stimulus generalization and discuss the theoretical implications of novelty/familiarity coding. Rats in Skinner boxes received clicker → shock pairings before generalization testing to a tone. Before clicker training, different groups of rats received preexposure treatments designed to systematically modulate the clicker and the tone's novelty and familiarity. Rats whose preexposure matched novelty/familiarity (i.e., either both or neither clicker and tone were pre-exposed) showed enhanced suppression to the tone relative to rats whose preexposure mixed novelty/familiarity (i.e., only clicker or tone was pre-exposed). This was not the result of sensory preconditioning to clicker and tone.

Key Phrases: novelty, familiarity, recognition memory.

Familiarity-Based Stimulus Generalization of Conditioned Suppression.

An understanding of animals' ability to discriminate novel from familiar stimuli is central to our understanding of recognition memory (e.g., Mackintosh, 1987; Mandler, 1980) and has implications for our understanding of stimulus representation (e.g., Gaffan, 1974; Honey, 1990; Honey, Horn, & Bateson, 1993; McLaren & Mackintosh, 2002). Much understanding of animals' novelty/familiarity discrimination comes from studies of rodents' spontaneous object recognition (e.g., Olarte-Sanchez, Amin, Warburton, & Aggleton, 2015; Whitt & Robinson, 2013). An alternative measure of animals' appreciation of novelty/familiarity, which has enjoyed rather little experimental attention, comes from experiments using a generalization test (e.g., Best & Batson, 1977; Honey, 1990; Robinson, Whitt, Horsley, & Jones, 2010; see also Iordanova & Honey, 2012).

Stimulus generalization refers to the finding that an animal's behavior, established to one stimulus may be elicited by other stimuli too (see, e.g., Guttman & Kalish, 1956; Hanson, 1959). Formal statements of learning (e.g., Harris, 2006; McLaren & Mackintosh, 2002; Pearce, 1994; Rescorla, 1976) differ in aspects of their conceptions of stimulus generalization but concur on its being based on notional sets of representational elements. For example, a rat's Pavlovian conditioned response might generalize from an auditory conditioned stimulus (composed of the representational elements, '1', '2', '3', and '4') to a second, similar, auditory stimulus (composed of the representational elements ('3', '4', '5', and '6') because they have,

in common, a proportion of shared representational elements (i.e., '3' and '4'). We may think of representational elements as being, within the limits of the sensory systems of the organism, an approximation of the physical characteristics of the conditioned stimulus. However, it has been claimed that a stimulus familiarity dimension can mediate generalization among stimuli, independently of their physical similarity (e.g., Best & Batson, 1977; Gaffan, 1974; Hall, 2001; Honey, 1990; Honey et al., 1993). Within the conception above, a novel stimulus might include an additional representational element, '7' and a familiar stimulus might include an additional representational element '8'. They could then affect generalization as physically-based representational elements are assumed to.

Based on an original demonstration by Honey (1990), Robinson et al. (2010) provided direct evidence for that suggestion. Two group of rats received extensive exposure to either two auditory stimuli, A and B, or to only stimulus B. The treatment was intended to modify stimulus generalization by making A and B more alike (for the A and B group) or less alike (for the B alone group). This was evaluated by using stimulus A as the conditioned stimulus in a shock-reinforced, conditioned suppression treatment before the assessment of conditioned responding to B in a separate and subsequent generalization test. The group whose preexposure treatment rendered both A and B familiar demonstrated more marked transfer of the conditioned response from A to B than in the alternative group whose preexposure treatment rendered only B familiar. It is important to note that, this

finding in general could be the result of either enhanced generalization in the A-B group; decreased generalization in the B-only group; or a mixture of an enhancement and a decrement in the two groups. For brevity's sake we will describe only familiarity-based stimulus generalization.

The idea that stimulus familiarity is encoded along with physically based representational elements has rather broad implications for our understanding of stimulus representation, discrimination learning and recognition memory. Because of this, we sought to confirm the findings of Robinson et al. (2010) in the current report. The first pair of experiments provide further evidence of, and an extension of, the Robinson et al. finding. The third experiment examined an alternative explanation of familiarity generalization based on sensory preconditioning. The logic of applying generalization testing here rests on the assumption that conditioning will not be sufficient to make stimulus A appreciably familiar. For that reason, the number of conditioning trials was kept relatively low, though with a relatively strong shock-reinforcer to support a reasonable level of conditioning. Experiments 1 and 3 used four conditioning trials (cf., Robinson et al.). Experiment 2 used only two conditioning trials, which should better retain A's relatively novelty, albeit at the potential cost in a reduction of suppression available to generalize to B during testing. Conditioning was assessed by reference to suppression of instrumental responding. Experiments 1 and 3 used a lever-press instrumental response and Experiment 2 used a food-tray entry instrumental response. Lever

press responding produced less varied response rates than food-tray entry but both measures were suitable for the evaluation of generalization testing.

Experiment 1

The experimental series reported here was designed to confirm and extend Robinson et al.'s (2010) demonstration of familiarity-based stimulus generalization in a conditioned suppression procedure with rat subjects. Experiment 1 was intended merely to confirm the reliability of Robinson et al.'s basic procedure before its further examination in the remainder of the experimental series. Robinson et al.'s demonstration of familiarity-based generalization comes from two groups of rats that had received sham brain surgery to permit comparison with a separate pair of rats that had received excitotoxic cortical lesions. It is unlikely, though possible, that the rats' sham surgery had some unintended collateral effect on familiarity-based generalization finding. Experiment 1's demonstration employed rats that had not received surgery of any type and should, thus, yield fully generalizable findings.

Experiment 1 employed a conditioned suppression procedure in rats and its design is summarized in Figure 1. During conditioning, group CT and group T, received pairings of a clicker (C) and a brief foot-shock. During testing, generalization of responding, established to C, was assessed to a tone (T). Before those stages, both groups of rats received preexposure to T; but only group CT was given presentations of C. Thus, during the test, for group CT, both C and T would be familiar but for group T, only T would be familiar. Pairings of C and the shock

during conditioning may also make C familiar. To limit the extent of C's familiarity for group T, only four pairings of C and the shock were given. If generalization from C to T were based only on physical stimulus features (i.e., those common to C and T), there would be no difference in the generalized response during test. However, if Robinson et al.'s (2010; see also, Best & Batson, 1977; Iordanova & Honey, 2012; Honey, 1990) finding is replicable, group CT's responding to T should be of greater magnitude than group T's.

Method

Subjects & Apparatus.

Experimentally naïve, male, Lister hooded rats (*Rattus norvegicus*; Charles River, UK) served as subjects. When experimentation was not occurring (see Procedure below), rats were held in an air-conditioned vivarium that was illuminated by fluorescent strip lights between 0700 - 1900. Temperatures were maintained between 20 and 23°C. Rats were housed in acrylic cages. To provide rats with environmental enrichment, each cage contained a large cardboard cylinder, and all rats were pair housed. Cages contained fresh wood-chip bedding and tap water was always available. Rats received free access to food (Harlan Teklad, Bicester, United Kingdom) in the cages until one week before the experiment began. At that time, rats' weights were recorded (mean: 247 g; range: 229 – 268 g) and food access was thenceforth restricted. Measured amounts of food were given once daily to reduce gradually rats' weights to between 80 % and 90 % of their baseline

weight. To promote healthy growth increase during the experiment, rats' target weight was increased each week. The rate of that increase was based on the mean weekly weight change of a separate group of rats that had been allowed unrestricted access to food and water in our vivarium. Sixteen rats began the experiment but due to a failure of the lever in one Skinner box, it was necessary to exclude one rat from each group, (i.e., *n*s = 7).

Eight identically specified Skinner boxes (MED Associates, St Albans, VT) were used (30.0 cm 24.0 cm x 20.5 cm high), which were normally not illuminated. Each was individually housed in a sound- and light-attenuating shell. The ceiling and 30.0-cm Skinner box walls (one of which served as a door) were constructed from clear polycarbonate. The 24.0-cm walls were constructed from metal plates. One wall was equipped with a recessed tray to which 45-mg food pellets (Noyes, Lancaster, NH) could be delivered. An infrared beam was sent from one lateral side of the food tray and received on another. Beam interruption could be recorded as a response (henceforth, food-tray activity). A lever was located to the left of the food tray, depression of which actuated a switch that could also be used to record responding (henceforth, lever pressing). The lever could be retracted into the wall to prevent lever pressing. Two lamps, whose 2.5-cm diameter, circular covers were composed of opaque plastic, were located symmetrically adjacent to the food tray (10.5 cm from the floor and 16.0 cm apart, center-to-center). A third lamp was located on the opposite metal wall, centrally and 17.5 cm above the floor. The lamp

was shrouded in a metal hood that could direct light toward the ceiling. None of the lamps were operated in any of the experiments reported here.

A heavy-duty relay, located on the outer side of the wall, could be operated at 10 Hz to produce an 80-dB (re. Scale A) train of clicks (henceforth, C). A loud speaker, located on the wall opposite the food tray, could be used to present a 2-kHz and <85-dB pure tone (henceforth, T). Background noise (principally provided by an exhaust fan located in the shell) was 65 dB. C and T were of 30-s duration.

The floor was constructed from nineteen, 4.8-mm diameter, stainless-steel rods that ran parallel to the metal walls. Rods were spaced 1.6 cm apart, center-to-center. The floor could be electrified by a scrambled 0.5-s, 1.0-mA current (MED Associates, St Albans, VT, ENV-414SA) to produce a foot-shock. Experimental events were controlled and recorded with a Microsoft Windows-based personal computer that used the MED PC programming language. All apparatus was held in a quiet laboratory illuminated by ceiling-mounted fluorescent lamps.

Procedure.

Baseline Training.

Lever pressing was established to assess the fear responding (suppression of responding) during the test. Initially the lever was retracted and rats were given response-independent food pellets according to a 60-s, fixed-interval schedule. On the following session, the lever was extended into the box and rats could earn pellets according to variable-interval (VI) schedules. By the end of Baseline Training,

rats' lever pressing was reinforced according to a VI-60 schedule but richer schedules were used earlier in training. The lever pressing VI-60 schedule was operational throughout the remainder of the experiment. Rats received three 1-hr sessions of VI-60 Baseline Training sessions before progression to the preexposure stage.

Preexposure.

Rats were divided into two groups, group CT and group T that were matched according to their response rates from Baseline Training. During each of six sessions group CT was exposed to C and T each eight times. On the 1st, 4th and 5th sessions the sequence was T C C T T C C T T C C T T C C T; on the other three sessions the sequence was C T T C C T T C C T T C C T T C. Group T's treatment differed from group CT's only in that C was deleted. Group CT and group T were run on separate sessions to prevent group T inadvertently hearing C. On half the preexposure days, group CT was run before group T. The session duration was around 80 minutes. Inter-trial intervals (ITIs) varied around means of 280 s and 560 s for, respectively, group CT and group T.

Conditioning.

Conditioning was intended to establish a response (suppression of lever-press responding) to C. Two 1-hr sessions were given during the conditioning stage. In each, C was presented twice, co-terminally with the shock. Trials began 570 s and 2370 s from the session's beginning. A session was subsequently given to allow

responding to recover; food pellets were earned on the VI-60 schedule but no other stimuli were scheduled to occur.

Test.

The test stage was intended to examine differences in the (generalized) responding exhibited to T by group T and group CT. T was presented three times in a single session. The ITI varied around a mean of 280 s.

Data Treatment.

A variety of appropriate parametric analyses were used for null-hypothesis testing. Tests evaluated two-tailed hypotheses and alpha = .050. A Bayesian analysis supplemented the interpretation of a key null result (JASP (Version 0.7.5.5) [Computer software]. Amsterdam, The Netherlands). Partial eta squared (η_p^2) was used to represent main effect and interaction effect sizes. Standardized 90% confidence intervals for η_p^2 were computed using the methods described by Kelley (2007).

Results & Discussion

Baseline training proceeded successfully. Responding during the first four trials of preexposure is summarized in Table 1. The introduction of C to group CT during preexposure resulted in some transitory suppression. Analysis of variance (ANOVA) yielded a significant trial main effect, $F(3, 18) = 10.3$; $p < .001$; $\eta_p^2 > .631$, 90% CI [.29, .72]. For both groups, the introduction of T during preexposure resulted in a similar disruption of responding. ANOVA yielded a significant trial

main effect, $F(3,36) = 3.4$; $p < .030$; $\eta_p^2 > .219$, 90% CI [.01, .35], but no group main effect nor Group x Trial interaction, both Fs < 1. A notable implication of this evidence of unconditioned suppression, and its habituation, is that it may modify the conditioned suppression seen during the subsequent conditioning and test stages.

Responding to C during its four conditioning pairings with the shock was almost completely suppressed by the end of that stage but, earlier in that stage, suppression to C was less marked in group CT (mean rpm rates: 22, 23, 4, 2; SEMs: 2.6, 1.8, 1.2, 0.9) than in group T (mean rpm rates: 14, 1, 1, 0; SEMs: 2.6, 1.8, 1.2, 0.9). ANOVA yielded main effects of both trial, $F(3, 36) = 42.3$; $p < .001$; $\eta_p^2 > .779$, 90% CI [.64, .83], and group, $F(1, 12) = 47.3$; $p < .001$; $\eta_p^2 > .798$, 90% CI [.53, .87], and an interaction between those variables, $F(3, 36) = 13.6$ $p < .001$; $\eta_p^2 > .530$, 90% CI [.29, .63]. Between-group simple main effect (SME) analysis, which used the common error-term, yielded reliable group differences at Trials 1 and 2, smaller $F(1,48) = 11.3$; $p < .010$, but at neither Trial 3 nor Trial 4, larger $F(1, 48) = 2.3$; $p > .050$. The pattern of results is most simply understood as reflecting group T's initial unconditioned suppression to C, like that seen during preexposure to C by group CT, and its gradual replacement by conditioned suppression. For group CT, preexposure to C allowed unconditioned suppression to habituate and its changes reflect only the acquisition of conditioned suppression.

The data of principle interest, those of the test of T, are summarized in

Figure 1. Suppression was relatively great on the first trial in both groups but decreased over the course of testing. However, the level of suppression throughout the test was more marked in group CT than in group T. That impression was confirmed using ANOVA that yielded main effects of group, $F(1, 12) = 5.9$; $p < .033$; $\eta_p^2 > .328$, 90% CI [.02, .56], trial, $F(2, 24) = 9.4$; $p < .001$; $\eta_p^2 > .439$, 90% CI [.15, .58], but no interaction between those factors, $F(2, 24) = 1.4$; $p > .273$. An estimate of baseline response rates was made using the response rates during the 30-s period immediately preceding each of the tone presentation and these data are summarized in Table 2. ANOVA on these data, having the same format as that of the test data, yielded a main effect of trial, $F(2, 24) = 4.5$; $p < .023$; $\eta_p^2 > .272$, 90% CI [.02, .44] but no main effect of group nor Group x Trial interaction, *F*s < 1.

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FIG 1 ABOUT HERE

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The results of Experiment 1 provide a replication of Robinson et al.'s (2010) demonstration of familiarity-based generalization in surgically naive rats. This procedure parallels findings in conditioned taste aversion (Best & Batson, 1977) and appetitive conditioning (Honey, 1990). Group CT's preexposure treatment involved presentation of both C and T and was designed to ensure those stimuli were both encoded as familiar. In contrast, group T's preexposure treatment was designed to make C's and T's coding incongruent; that is, with T familiar and C novel. Based on

standard assumptions, C and T will have a set of common representational elements that govern stimulus generalization to the same extent in both groups. The fact that group CT's level of suppression was greater than group T's suggests that, if standard assumptions are correct, some additional process was occurring to enhance generalization from C to T in group CT – that process could be the result of generalization based upon novelty or familiarity coding. However, several other factors that could affect test performance to T will be considered before accepting that interpretation. First, unconditioned suppression to T was detected during preexposure, which could have certainly have affected test performance to T (i.e., the generalized fear response could be contaminated by unconditioned suppression; see, e.g., Robinson, Sanderson, Aggleton, & Jenkins, 2009; Jones, Whitt, & Robinson, 2012). But because both groups received preexposure to T, and because the course of habituation of unconditioned suppression was similar, this seems unlikely to generate the crucial group difference. One might anticipate that group CT's habituation of unconditioned suppression to C might generalize to T, being mediated by a subset (x) of shared representational elements, and reduce suppression relative to group T. If such a process did occur, we did not detect it during preexposure and, of course, that process would have worked against -- not in favor of -- the obtained group difference. Neither account based on unconditioned suppression appears to provide a suitable account of the results.

Second, any account based upon latent inhibition (e.g., Lubow & Moore,

1959), either of C or of the subset of features (x) shared by C and T, appears similarly inadequate in explaining the results. Group CT's preexposure to C might reduce C's capacity to govern responding in that group but that would act against the observed group difference. Here, the set of x features that mediate generalization may lose more associability in group CT than in group T – during preexposure x was presented twice as often in group CT than in group T (cf., Bennett, Wills, Wells, & Mackintosh, 1994; McLaren & Mackintosh, 2000). Thus, like the habituation account, this latent inhibition account fails to produce a realistic alternative account of the main findings because it predicts the opposite result to our findings.

Experiment 2

Experiment 1 successfully repeated Robinson et al.'s (2010) demonstration of familiarity-based generalization in surgically naive rats. We also saw that considerations of group differences in both habituation of conditioned suppression to the test stimulus, T or to differences in latent inhibition (e.g., Lubow & Moore, 1959) to the conditioned stimulus, C, were unable to account for the findings of Experiment 1. But in Experiment 1, the relative amounts of generalization were restricted to only two cases: one in which C and T were familiar (group CT) and one in which C was novel and T was familiar (group T). Experiment 2 sought to replicate the main finding of Experiment 1 and to extend the design to include an additional pair of groups (group 0 and group C; see Figure 2). Group 0 received neither C nor

T during preexposure, whereas group C received preexposure to C only.

One way to anticipate the results of Experiment 2 is to think of two of the groups as having equivalent (groups 0 and CT) or distinct (group C and T) preexposure treatments, (cf., Honey & Hall, 1989; Ward-Robinson & Hall, 1998). Thus, being agnostic about the relative contributions of putative familiarity and/or novelty based stimulus generalization, we might simply expect greater generalization in the aggregate equivalent treatment relative to the aggregate distinct treatment. Group-by-group test predictions are also possible; however, the results of Experiment 1 warn us of the danger of comparing groups whose preexposure treatments produce different levels of unconditioned suppression to T. Thus, comparison in the of pairs of groups whose treatment is matched for preexposure to T (i.e., group CT versus group T and group 0 versus group T) will allow fair examinations of familiarity-based generalization.

Method

Subjects & Apparatus

32 rats served as subjects. Their strain, supplier and maintenance were the same as in the previous experiment. Before food restriction began, rats' mean weight was 274 g (range: 244 – 304 g). The apparatus was that used in the previous experiment.

Procedure

Baseline Training.

Food-tray activity was used as the instrumental response in place of the lever press response used in Experiment 1. A rat's entry into the food tray would break the infrared beam that crossed from one side to the other (see Experiment 1, Subjects & Apparatus). Each beam break was recorded as an instrumental response. Our expectation was that this instrumental response would be acquired more quickly than the lever press training, thereby reducing the time rat spent being food restricted. There were two 1-hr sessions of Baseline Training. By the end of Baseline Training, rats' responses were reinforced according to a VI-60-s schedule, but richer schedules were used earlier in training. The VI-60-s schedule was operational throughout the remainder of the experiment.

Preexposure.

Rats were assigned to one of four groups (*n*s = 8), matched according their Baseline Training response rates. Group CT and group Ts' treatments were identical to their namesakes in Experiment 1. Group C's treatment differed from group T's only in that C, and not T, was presented; group 0 received neither C nor T. For group C and group T, the mean ITI was 560 s; for group CT it was 280 s. The session duration was around 80 minutes.

Conditioning.

For all groups, a single 1-hr session was given in which C was presented co-terminally with the shock. Two such trials were given occurring 570 s and 2370 s into the session. A session was given subsequently, intended to allow responding to

stabilize; food pellets were earned on the VI-60 schedule but no other stimuli were scheduled.

Test.

The test stage was intended to examine the extent of generalization of responding from C to T. Eight presentations of T were given. The ITI varied around a mean of 280 s.

Results & Discussion

Baseline Training preceded without incident. As in Experiment 1, the introduction of C during preexposure resulted in some changes in suppression of responding in group CT and group C. The first four trials of preexposure are summarized in Table 1. ANOVA of those data produced no group main effect, $F < 1.0$, but a main effect of trial, $F(3, 42) = 7.9$; $p < .001$; $\eta_p^2 > .363$, 90% CI [.14, .48] and a Group x Trial interaction, $F(3, 42) = 4.5$; $p < .008$; $\eta_p^2 > .243$, 90% CI [.04, .37]. That interaction yielded a SME at Trial 2, $F(1, 50) = 6.5$; $p < .025$; no other SME was reliable, largest $F(1, 50) = 3.0$; $p > .050$. Introduction of T also caused an initial suppression in group CT and group T. ANOVA of those data yielded a main effect of trial, $F(3, 42) = 16.3$; $p < .001$; $\eta_p^2 > .538$, 90% CI [.32, .63], but neither the group main effect nor its interaction with trial was reliable, smaller $p > .266$.

Responding during conditioning followed the same general patterns as conditioning from Experiment 1. Mean response rates from each of the two trials of conditioning were: for group CT, 57 and 61 rpm (SEMs: 9.5, 8.9); for group 0, 20

and 11 rpm (SEMs: 9.5, 8.9); for group C, 43 and 63 rpm (SEMs: 9.5, 8.9); and for group T, 28 and 15 rpm (SEMs: 9.5, 8.9). Thus, as in Experiment 1, rats whose preexposure included C (group CT and group C), showed higher response rates during that stimulus' conditioning presentation than the other two groups. And, again, the difference was apparent before the first shock presentation (i.e., on the first C conditioning trial), which suggests that an unconditioned response to C was responsible for suppression of responding. ANOVA computed with those data revealed neither the main effects nor interaction for trial, smaller $p > .280$, but a reliable group main effect, $F(3, 28) = 10.9$; $p < .001$; $\eta_p^2 > .538$, 90% CI [.26, .64]. Corrected tests failed to detect reliable differences between groups C and CT and between groups 0 and T, *t*s < 1. The four other permutations of comparison were all found to be reliable, smallest $t(14) = 3.6$; $p < .015$.

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FIG 2 ABOUT HERE

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Data from the test with T are summarized in Figure 2. The leftmost panel summarizes data from the pair of groups for whom T was familiar at the beginning of the test (i.e., for these groups T was included in preexposure); the rightmost panel summarizes data from the pair of groups for whom T was novel at the beginning of the test (i.e., for these groups T was not included in preexposure). Thus, within each panel, each pair of groups are matched in terms of likely

unconditioned suppression to T, obtaining an unbiased measurement of novelty/familiarity generalization. As might be expected, there was some indication that response rates changed during testing and there was a tendency for rats for whom T was novel at test (rightmost panel) to show more suppression of responding during T than rats for whom T was familiar (leftmost panel). Of more significance was the tendency for there to be most suppression in groups whose preexposure to C and T was matched (i.e., groups CT and 0; mean rpm: 34; SEM: 2.91) than mixed (i.e., groups T and C; mean rpm: 47; SEM: 3.72); $t(31) = 2.7$; $p < .011$; $\eta_p^2 > .238$, 90% CI [.03, .37].

A more detailed analysis of T responding during the test was performed by ANOVA with the four groups coded as having T novel/familiar at the beginning of the test (i.e., C and 0 versus CT and T) and C novel/familiar at the beginning of the test (i.e., T and 0 versus CT and C). Of most significance was the reliable T Novel/Familiar x C Novel/Familiar interaction, $F(1, 28) = 8.4$; $p < .007$; $\eta_p^2 > .231$, 90% CI [.04, .40], which is decomposed in the next paragraph. The ANOVA also revealed a reliable main effect of block, $F(3, 84) = 10.5$; $\eta_p^2 > .274$, 90% CI [.13, .37] -- reflecting an overall tendency for response rates to increase over testing -- and a main effect of T's being novel/familiar during preexposure, $F(1, 28) = 5.4$, $p < .028$; $\eta_p^2 > .162$, 90% CI [.01, .34]. The main effect of C's being novel/familiar was not reliable, $F < 1.0$; however, the C Novel/Familiar x Block interaction was reliable, albeit with an uncertain effect size and no obvious theoretical significance, $F(3, 84) =$

2.7; $p < .047$; $\eta_p^2 > .090$, 90% CI [.00, .17]. Inspection of the means indicated that the interaction was the consequence of groups for whom C was familiar showing an orderly increase in response rate over the four blocks, whereas groups for whom C was novel showed a relatively abrupt increase from the first to the second block. Neither the T Novel/Familiar x Block, $F(3, 84) = 1.5$, $p > .210$, nor the C Novel/Familiar x T Novel/Familiar x Block, $F < 1.0$, was reliable.

The source of the ANOVA's reliable T Novel/Familiar x C Novel/Familiar interaction was examined with two additional ANOVAs, one for the pair of groups for whom T was familiar (i.e., groups CT and T); the other for the pair of groups for whom T was novel (i.e., groups C and 0). The first of this pair of ANOVAs found a reliable main effect of block, $F(3, 42) = 4.1$; $p < .012$; $\eta_p^2 > .229$, 90% CI [.03, .35] and an unreliable, but modestly sized, effect of the difference between groups CT and T, $F(1, 14) = 3.6$; $.077 < p < .078$; $\eta_p^2 > .206$, 90% CI [.05, .95]. The Group x Block interaction was unreliable, $F(3, 42) = 1.8$, $p > .168$. The second of this pair of ANOVAs found a reliable main effect of the difference between groups T and 0, $F(1, 14) = 4.8$; $p < .045$; $\eta_p^2 > .258$, 90% CI [.00, .49] and a reliable main effect of block, $F(3, 42) = 10.1$; $p < .001$; $\eta_p^2 > .420$, 90% CI [.19, .53]. The Group x Block interaction was unreliable, $F(3, 42) = 1.1$, $p > .324$. SME analyses using the common error terms indicated that group CT and group T differed on blocks 2 and 3, smaller $F(1, 14) = 2.7$; $p < .008$; $\eta_p^2 > .205$, 90% CI [.00, .41] and that groups 0 and C differed on blocks 3 and 4, smaller $F(1, 14) = 3.7$; $p < .001$; $\eta_p^2 > .256$, 90% CI [.0,

.45]. Response rates during the 30-s period immediately preceding each of the tone presentation and these data are summarized in Table 2. ANOVA on these data, generated a main effect of block, $F(3, 84) = 25.8$; $p < .001$; $\eta_p^2 > .479$, 90% CI [.33, .56] but no main effect of group nor Group X Block interaction, respectively, $F(3, 28) = 1.3$; $p > .281$; $\eta_p^2 < .127$, 90% CI [.00, .05], and $F(9, 84) = 1.7$; $p > .095$; $\eta_p^2 < .155$, 90% CI [.00, .19].

The results above confirm those of Experiment 1 and Robinson et al. (2010) in showing the familiarity-based generalization of conditioned suppression. They extend those findings in demonstrating greater familiarity-based generalization in group 0 than in group C, complementing a finding reported by Honey (1990) in an appetitive conditioning procedure with rats. This pair of groups are matched in their experience of T during the test, a prerequisite for the measurement of suppression without concerns about contamination by unconditioned suppression. They may be taken as representing differences in generalization from novel-to-novel (group 0) and familiar-to-novel (group C), paralleling group CT (familiar-to-familiar generalization) and group T (novel-to-familiar generalization).

We discussed some explanations of the group CT-group T difference, not reliant on familiarity-based generalization and concluded that they were without merit. Are there more realistic alternative accounts of the group 0-group C difference? We considered a potential role of latent inhibition (e.g., Lubow & Moore, 1959) in generating differences in suppression on test in Experiment 1 and

concluded that for this case of the group CT versus group T comparison, any latent inhibition that would accrue to C from the preexposure treatment of group CT would reduce C's capacity to gain associative strength. This would, therefore, offer little generalized responding to T. Thus for the group CT versus group T comparison, any generalization of latent inhibition would work against the observed effect, which may, therefore, be safely accepted. However, direct latent inhibition to C may reduce the acquisition of associative strength for group C, thereby reducing the availability of associative strength to generalize to T. The comparison of group C with group 0 is, therefore, potentially biased because of the absent opportunity for latent inhibition to C in group 0. Both groups 0 and C will also be susceptible to unconditioned suppression on test to T, but this should be matched: T is novel for both groups. But we saw that group C's suppression to C during preexposure habituated. We need only assume that there was some generalization of habituated suppression from C to T to accommodate the finding that group C showed less suppression than group 0 on test.

While the alternative accounts of the group-0 versus group-C difference is amenable to alternative explanations based on generalized latent inhibition or habituation of suppression, it seems arbitrary to accept the group-CT versus group-T difference as demonstrating familiarity-based generalization but to doubt the complementary, group-0 versus group-T difference. Or put another way, why should familiar-to-familiar generalization (i.e., group CT versus group T) be effective

but novel-to-novel generalization (i.e., group 0 versus group T) not be effective? And the finding that the aggregated data from groups 0 and CT (matched for the novelty/familiarity to C and to T) was more suppressed than the aggregated data from groups C and T (with mixed novelty/familiarity to C and to T) is immune to any overall influence of generalized latent inhibition or unconditioned suppression. This is because the effects of habituation to C and to T are orthogonal to the observed pattern of suppression, which is only interpreted as familiarity-based generalization. Our conclusion, therefore, is that the results of Experiment 2 are most parsimoniously interpreted as showing familiarity-based generalization.

Experiment 3

Experiment 3 sought to experimentally examine an alternative account of the suppression seen in group CT in Experiment 1 and 2. There are parallels in a sensory preconditioning procedure and that of group CT's treatment in Experiment 1 and 2. For example, Ward-Robinson and Hall (1996) gave rats pairings of a compound audio-visual stimulus before establishing one element as a conditioned stimulus and finally measuring conditioned responding to the other. In his analysis of Honey's (1990) report, Hall (2001) maintained that there is no obligation for us to accept familiarity-based generalization when an account simply based on sensory preconditioning suffices. For example, if the treatment given to group CT, allows associations to form between C and T during preexposure, sensory preconditioning could occur. Conditioning to C could result in T gaining its own associative strength

as its representation is activated by the presentation of C (e.g., Dwyer, Mackintosh, & Boakes, 1998; Holland, 1990). An alternative to such a mediated conditioning mechanism of sensory preconditioning is one operational on test (see, e.g., Ward-Robinson & Hall, 1996 for discussion). Here the presentation of T associatively activates the representation of C, via the association established during preexposure. Because C's conditioning treatment will have established an association with the shock, T too, will be able to provoke conditioned responding. Neither such process is possible for the comparison, group T.

Experiment 3, which is summarized in Figure 3, sought to experimentally examine this suggestion by varying the ITI between C and T trials during preexposure. One group of rats (group CT 280) received a similar preexposure treatment to group CT in Experiments 1 and 2. A second group of rats (group CT 140) received a similar treatment to group CT 280's except that their ITI was halved. Our prediction was that, if group CT 280's test suppression was based on learning about the co-occurrence of C and T, albeit over a fairly long ITI, then the reduction of the ITI for group CT 140 will enhance test suppression. A third group (CT 420) received a treatment similar to group CT 280s but with a longer ITI to reduce any learning about the co-occurrence of C and T during preexposure. Two additional groups (groups 0 and T) were included to provide references for familiarity-based generalization.

Method

Subjects & Apparatus

40 experimentally naïve rats served as subjects. Their strain, supplier and maintenance were the same as in the previous experiments. Before food restriction began, rats' mean weight was 283 g (range: 255 – 320 g). The apparatus was that used in the previous experiments.

Procedure

Baseline Training.

Lever pressing was used as the response and was established as in Experiment 1. This change was based on the observation that although the beam-break instrumental response used in Experiment 2 was established quickly it tended to be more variable than lever pressing.

Preexposure.

Rats were assigned to one of five groups (*n*s = 8), matched according their Baseline Training response rates. Group 0 and group T received a similar stimulus preexposure treatment to their namesakes from previous experiments. The session duration was 40 minutes and group T's ITI varied around a mean of 280 s. Three groups of rats received preexposure to both T and C, like that of group TC from previous experiments. The groups' mean ITIs were 140 s (group CT 140), 280 s (group CT 280) and 420 s (group CT 420). Group CT 140's, CT 280's and CT 420's session durations were, respectively, 40, 80 and 120 minutes.

Conditioning.

Rats received two conditioning sessions in which C was paired co-terminally with a shock. These sessions were 80 minutes' duration and contained two trials; the first trial occurred at 570 s, and the second at 2370 s from the beginning of the session. After the conditioning sessions, all rats received one VI-60 lever press session to recover lever pressing after conditioning. The increase in the number of trials to four, from the two trials given in the previous experiment, was intended to produce more pronounced suppression to T during testing and matches that of Experiment 1. It was anticipated that this might allow better detection of the transfer of familiarity-based generalization.

Test.

The test stage examined the extent of generalization of responding from C to T and the level of suppression that had been established during conditioning. Eight presentations of T were given and the ITI varied around a mean of 280 s.

Results & Discussion

Baseline training and preexposure proceeded without incident and changes in response rates were similar to previous experiments. Data from the first four trials of preexposure are summarized in Table 1. The differences in ITI appeared to produce no differences in the habituation of suppression to C in the three CT groups. ANOVA on the C data yielded main effects of trial, $F(3, 63) = 35.2$; $p < .001$; $\eta_p^2 > .62$, 90% CI [.48, .69], but no main effect of group, $F(2, 21) = 2.5$; $p > .101$, nor Group x Trial interaction, $F < 1.0$. The corresponding ANOVA on the T

data for the four groups whose preexposure included T produced main effects of group, $F(4, 35) = 3.2$; $p < .023$; $\eta_p^2 > .272$, 90% CI [.02, .38] and trial, $F(3, 105) = 4.4$; $p < .007$; $\eta_p^2 > .112$, 90% CI [.02, .19] but no Group x Trial interaction $F(12, 105) = 1.6$; $p > .100$. The source of the group main effect was examined using corrected tests but no individual comparison was significant (largest $t(14) = 2.9$; $.073 > p > .071$).

As was the case in the previous two experiments, the effects of the introduction of the C conditioning trials varied across groups: Groups unfamiliar with C from their preexposure exhibited pronounced unconditioned suppression that was apparently replaced with conditioned suppression (i.e., Groups 0 and T showed low levels of suppression on all four trials). The three CT groups responded at an initially high rate, which steadily reduced over the four trials. Mean rpm rates for the four C conditioning trials were: Group CT 140: 11, 13, 3, 0 (SEMs: 2.1, 1.8, 1.5, 0.3); Group CT 280: 15, 12, 4, 1 (SEMs: 2.4, 1.9, 1.3, 0.4); Group CT 420: 12, 13, 3, 1 (SEMs: 2.2, 3.3, 1.6, 0.5); Group 0: 1, 0, 0, 0 (SEMs: 0.3, 0.3, 0.0, 0.3); Group T: 1, 1, 0, 2 (SEMs: 1.0, 0.5, 0.0, 0.6). ANOVA on these data yielded main effects of group, $F(4, 35) = 19.9$; $p < .001$; $\eta_p^2 > .694$, 90% CI [.50, .76], trial, $F(3, 105) = 37.1$; $p < .001$; $\eta_p^2 > .513$, 90% CI [.39, .59] and a Group x Trial interaction, $F(12, 105) = 6.1$; $p < .002$; $\eta_p^2 > .413$, 90% CI [.22, .45]. That Group x Trial interaction was subjected to a SME analysis, with a common error-term, and revealed significant group effects at trials 1 and 2, smaller $F(35, 105) = 20.1$; $p < .001$ (at trial 2), but

failed to detect a difference at trials 3 and 4, larger $F(35, 105) = 1.5$; $p > .065$ (at trial 3). Corrected tests at trial 2 revealed that none of the three CT groups differed, all *t*s < 1 but that group 0 differed from the three CT groups, smallest $t(14) = 4.4$, $p < .002$ and that group T differed from the three CT groups, smallest $t(14) = 4.1$, $p < .001$.

The results of main interest are those from the test session (Figure 3). During the presentation of the tone, all but group T showed low levels of responding. Of most importance is the similar pattern of results in the three CT groups. ANOVA with trial and group confirmed these descriptions. There was a significant effect of trial, $F(3, 105) = 9.5$, $p < .001$; $\eta_p^2 > .21$, 90% CI [.09, .31], and of group, $F(4, 35) = 5.9$, $p < .001$; $\eta_p^2 > .40$, 90% CI [.13, .51], but no interaction, $F(12, 105) = 1.4$, $p > .169$. Corrected tests failed to find differences among the three CT groups and group 0, all ts < 1 but group T differed from all four of the other groups, smallest $t(14) = 3.2$, $p < .030$. A supplementary Bayes factor ANOVA was performed (JASP (Version 0.7.5.5) [Computer software]. Amsterdam, The Netherlands) on the three CT groups' data alone and showed the null model to be preferred over the group model by a Bayes factor of about three (BF01 > 3.153). The Bayes factor captures the relatively probabilities of the null hypotheses to the alternative hypothesis, with a factor of one signifying that each is equally likely. The value, here, indicates that the null hypothesis is over 3 times more likely than the alternative hypothesis for these data. A threefold Bayes factor has been suggested as a

meaningful in the interpretation of data (see, e.g., Rouder, Speckman, Sun, Morey, & Iverson, 2009; see also, Kruschke, 2013).

Baseline response rates were examined using the 30-s period immediately preceding each of the tone presentation and these data are summarized in Table 2. ANOVA on these data, yielded no group main effect, $F < 1$, nor block main effect, $F(3, 12) = 1.0$; $p > .376$; $\eta_p^2 < .029$, 90% CI [.00, .08], nor Group x Block interaction, $F(12, 105) = 1.4$; $p > .191$; $\eta_p^2 < .134$, 90% CI [.00, .14]. It is notable that the mean baseline response rates summarized in Table 2 exceed their corresponding mean rate during the test with the tone on some blocks; that is the tone appeared to elevate instrumental responding, rather than suppress it. This is probably less surprising than at first it seems because, after briefly eliciting unconditioned suppression, the tone unconditionally elevated responding. For example, the response rates during the six presentations of the tone on the final preexposure session, for groups CT and T, was 51.6 rpm with a corresponding baseline rate of 36.6 rpm, $t(15) = 5.2$, $p < .001$; $\eta_p^2 > .649$. Thus, the tone's unconditioned elevation is likely to offset the conditioned suppression that generalizes from the click during testing. And we may expect that full extinction will result in baseline:tone rpm ratios that approximate those seen at the end of preexposure (i.e., 7:5), rather than in parity.

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FIG 3 ABOUT HERE

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The results of Experiment 3 failed to confirm the suggestion that group CT's enhanced suppression was based on learning about the co-occurrence of C and T during preexposure, a process akin to sensory preconditioning (cf., Hall, 2001). By elimination, this supports the suggestion that test performance was based upon familiarity-based stimulus generalization, which does not predict that generalization will co-vary with ITI.

Although the logic of argument from sensory preconditioning is sound enough, it is notable that explicit manipulations of preexposure treatments indicate that sensory preconditioning is best achieved with no ITI -- that is, with the stimuli presented as a simultaneous compound (e.g., Rescorla, 1980; see also Honey & Bolhuis, 1997; Müller, Gerber, Hellstern, Hammer, & Menzel, 2000). Of course, such evidence does not preclude the establishment of suboptimal sensory preconditioning that could influence group CT’s suppression to T. However, sensory preconditioning has been reported to be fully absent when separated by an interval of only 14 s (Wynne & Brogden, 1962); and routinely-used unpaired control treatments receive ITIs less than the 280 s used here (e.g., 240 s, by Talk, Gandhi, & Matzel, 2002). Based on these considerations and the results of Experiment 3, we assume that the ITIs used in all of the CT treatments far exceed that necessary to

produce sensory preconditioning.

As acknowledged in earlier experiments, in addition to potential modulation of the representation of familiarity of C and T, the preexposure stage offers the opportunity for the latent inhibition (e.g., Lubow & Moore, 1959) to C and for habituation of unconditioned suppression to T (e.g., Robinson, et al., 2009; Jones, et al., 2012). Both processes are potentially able to modulate responding to T during testing. We noted above, the preexposure treatment given to the three group CTs could latently inhibit C resulting in relatively weak transfer of suppression to T on test. Because the opposite result was found we may assume that, if this occurred, it was offset by a more powerful, opposing variable, such as familiarity-based generalization. Such a process is not expected in either group 0, or group T whose preexposure did not include C. The preexposure treatments for group T and the three CT groups, could allow unconditioned suppression to T to habituate. Indeed, this could provide an artefactual account for the strong suppression shown by group 0, but no such account can be applied to the differences between the CT groups and group T, whose preexposure treatment match exposure to T.

General Discussion

The experiments reported here obtained evidence that generalization of responding among a pair of auditory stimuli is modified by their familiarity (or novelty). In all experiments, generalization was greater when the auditory stimuli were matched for familiarity (either both stimuli were familiar or both stimuli were

novel) than when their familiarity was mixed (one was familiar, the other novel); that is, generalization occurred along a dimension of stimulus familiarity (cf., Best & Batson, 1977; Gaffan, 1974; Honey, 1990; Honey et al., 1993; Robinson et al., 2010). We saw also that familiarity-based generalization did not seem to be the result of sensory preconditioning occurring in group CT (cf., Hall, 2001).

The suggestion that novelty or familiarity act as standard elements in the representation of stimuli seems dysfunctional for the organism in certain experimental, and real-life, settings. For example, the discrimination of an experimental rat whose choice of only one of a pair of differently odored bowls results in food reinforcement (e.g., Birrell & Brown, 2000), should be compromised: Each bowl's odor begins the discrimination with novelty elements adding to the population of shared elements. Thus learning of the relationship between each odor and its outcome, be that reinforcement or non-reinforcement, will transfer to the alternative odor and reduce discrimination. Over the course of training, the novelty elements may become replaced by familiarity elements; but because the odors will have been exposed on each trial, they should be similarly familiar and the inappropriate transfer of learning about the outcome of each odor choice will continue. Of course, we need only assume that the contribution of such dysfunctional generalization is offset by larger, intrinsic differences in the pair of odors to successfully solve the discrimination.

Once it is accepted that novelty and familiarity enter into the representation

of a stimulus, standard assumptions about associative learning will accommodate our findings. We might think of stimuli C and T as having three separable populations of representational elements, corresponding to unique elements (respectively, 'c' and 't'), their shared elements ('x') and the presence of mutually exclusive elements that code for novelty or familiarity ('n' or 'f'). We coded the stimuli in Experiment 2 in this way and computed test values based on the Rescorla and Wagner (1972) model of associative learning. The simulation accurately captured the familiarity-based generalization and if the learning-rate parameter for 'n' exceeds that for 'f', the simulation accurately captures our observation that the group 0-group C difference was more pronounced than that of the group CT-group T difference. It is necessary to include both 'n' and 'f' representational elements: A simulation with 'f' but not 'n' produces the correct group CT-group T difference but fails to predict the group 0-group C difference; and a simulation with 'n' but not 'f' correctly predicts the group 0-group C difference but fails to predict the group CT-group T difference. Thus, from Rescorla and Wagner's point of view, familiarity-based generalization relies on both 'n' and 'f' elements and requires the learning-rate parameter for 'n' to exceed the learning-rate parameter for 'f'. Pearce's model (e.g., 1987) operates differently in its conception of stimulus generalization from Rescorla and Wagner's (1972). The generalization from C to T in the current experiments assumed by the Pearce model to be related to the proportion of common ('x') to unique elements ('c', 't', 'n', 'f'). If we conceive of C and T in the four

groups of Experiment 2 as having potential for five elements (i.e., 'c', 't', 'x', 'n' and 'f'), C and T have either 1/5 (groups C and T) or 2/5 (groups CT and 0) of elements in common and Pearce successfully predicts familiarity-based generalization. Unlike the Rescorla and Wagner model, it is unnecessary to include both 'n' and 'f' representational elements because similarity (and, therefore, generalization) is assumed to be symmetrical. But, like the Rescorla and Wagner model, the assumption that 'n' elements are more salient than 'f' elements yields the pattern of results seen in Experiment 2: That the group C and 0 difference was more pronounced than the group CT and T difference. This bias in the salience of 'n' and 'f' seems reasonable given that novel stimuli elicit marked overt orienting responses (e.g., Robinson, et al., 2009; Jones, et al., 2012).

How then might the code for novelty and familiarity be generated to allow its involvement in stimulus generalization? One position on familiarity encoding (e.g., McLaren & Mackintosh, 2002) is that subjects' initial reception of cues is variable, but that repeated exposure allows formation of a coherent network of intra-stimulus features, direct evidence being supplied by study of the effects of stimulus preexposure on subsequent conditioned responding (e.g., Fanselow, 1990; Killcross et al., 1998; Talk et al., 2002). Brandon, Vogel, and Wagner (2003) suggest ways that such intra-stimulus associations will tend to encourage qualitatively different patterns of activation to familiar stimuli than to novel stimuli that, in lacking intra-stimulus associations. One might instead suppose that the latencies associated

with the activation of robustly represented (familiar) and diffuse (novel) stimuli may be discriminable. For example, the rate of change in activity may be steeper for familiar stimuli than for novel stimuli (cf., Aggleton & Brown, 2006; Xiang & Brown, 1999); that is, both novel and familiar stimulus features may become activated to the same extent in a unit time by external stimulation but familiar stimulus features will have an additional source of activation: Internal activation provided by associated features. And again, one need only assume that such rate differences can affect stimulus generalization to accommodate demonstration of generalization along a familiarity continuum.

Experiment 3 challenged an account of familiarity-based generalization based on sensory preconditioning between C and T over the preexposure ITI (cf., Hall, 2001). However, it seems possible that even long ITIs could foster association between C and T if they are mediated by an intermediate representation of the context. Thus, group CT's preexposure treatment could foster formation of a T -> context -> C associative chain, which would be modified during conditioning by the addition of a terminal shock representation to create: T -> context -> C -> shock. For the central comparison group, group T, preexposure and conditioning would result in two separate associative chains: T -> context and C -> shock. Thus, on test T will provoke suppression in group CT but not in group T. This potential mechanism relies upon group T forming only a weak context -> C association during conditioning; and this is not implausible given the deliberately restricted

number of C -> shock trials given to retain C's novelty.

In addition, group CT could form the symmetrical associative chain (C -> context -> T), which could allow T to enter into association with the shock when its representation is activated by C during conditioning (cf., Dwyer et al., 1998; Holland, 1990; Ward-Robinson & Hall, 1996). However, group T's preexposure should also promote formation of a context -> T association, and because the context is actually present during conditioning it should activate the representation of T allowing it to also enter into a direct association with the shock. Thus, the context-mediated form of sensory preconditioning cannot operate during the conditioning stage. It is also possible to derive a form of sensory preconditioning analysis of the group CT, group T difference from mediated conditioning that could occur during preexposure. One version would be that the context could, increasingly over the course of preexposure, associatively activate C and T for group CT. This could allow the associatively activated representation of each stimulus to enter into excitatory association with the other on complementary trials (cf., Holland, 1990; Ward-Robinson & Hall, 1996; see also, Dwyer et al., 1998; and for a different analysis, Lin, Dumigan, Recio, & Honey 2016). Once it is allowed that C and T have become symmetrically associated in this way, both of the sensory preconditioning mechanisms discussed above are able to operate.

These variant sensory-preconditioning analyses are important because they accommodate the results of the key group CT versus group T comparison with no

necessity to assume that stimulus novelty or familiarity are represented in any special way or that they mediate generalized suppression. Having said all this, the findings that manipulations of the perirhinal cortex affect rats' performance both in the task reported here (Robinson et al., 2010), and in a broad range of recognition memory tasks (e.g., Albasser, Davies, Futter, & Aggleton, 2009; Baxter & Murray, 2001) encourage the view that the same psychological process is being affected. We might take recognition memory to be the discrimination between novel and familiar items (cf., Mackintosh, 1987; Mandler, 1980) and so, when taken together, the most natural interpretation of our results is one in terms of familiarity based stimulus generalization.

The notions of novelty/familiarity encoding described here have obvious parallels with theoretical conceptions of familiarity detection (e.g., Aggleton & Brown, 2006), which have been developed using quite different procedures from those described here, for example, spontaneous object recognition in rats (e.g., Olarte-Sanchez et al., 2015; Whitt, Haselgrove, & Robinson, 2012). The demonstrations of familiarity-based stimulus generalization reported here confirm those of Robinson et al., (2010), which also used conditioned suppression. And, in complementing findings from Best and Batson (1997) and Honey (1990) they present familiarity generalization as a general phenomenon that should be considered in theoretical statements on stimulus representation and discrimination.

References

Aggleton, J. P., & Brown, M. W. (2006). Interleaving brain systems for episodic and recognition memory. *Trends in Cognitive Sciences, 10*, 455-463. doi:10.1016/J.Tics.2006.08.003

Albasser, M. M., Davies, M., Futter, J. E., & Aggleton, J. P. (2009). Magnitude of the object recognition deficit associated with perirhinal cortex damage in rats: Effects of varying the lesion extent and the duration of the sample period. *Behavioral Neuroscience, 123*, 115–124.

Baxter, M. G., & Murray, E. A. (2001). Impairments in visual discrimination learning and recognition memory produced by neurotoxic lesions of rhinal cortex in rhesus monkeys. *European Journal of Neuroscience, 13*, 1228–1238.

Best, M. R., & Batson, J. D. (1977). Enhancing the expression of flavor neophobia: Some effects of the ingestion-illness contingency. *Journal of Experimental Psychology: Animal Behviour Processes, 3*, 132-143.

Birrell, J. M., & Brown, V. J. (2000). Medial frontal cortex mediates perceptual attentional set shifting in the rat. *Journal of Neuroscience, 20*(11), 4320-4324.

Davis, M. (1970). Effects of interstimulus interval length and variability on startle-response habituation in the rat. *Journal of Comparative and Physiological Psychology, 72*, 177-192. doi:10.1037/h0037208

Dwyer, D. M., Mackintosh, N. J., & Boakes, R. A. (1998). Simultaneous activation of the representations of absent cues results in the formation of an excitatory

association between them. *Journal of Experimental Psychology: Animal Behavior Processes, 24,* 163–171.

Fanselow, M. S. (1990). Factors Governing One-Trial Contextual Conditioning. *Animal Learning & Behavior, 18*, 264-270.

Gaffan, D. (1974). Recognition Impaired and Association Intact in Memory of Monkeys after Transection of Fornix. *Journal of Comparative and Physiological Psychology, 86*, 1100-1109.

Guttman, N., & Kalish, H. I. (1956). Discriminability and stimulus generalization. *Journal of Experimental Psychology, 51*, 79-88.

Hall, G. (2001). Perceptual learning: Association and differentiation. In R. R. Mower & S. B. Klein (Eds.), *Handbook of contemporary learning theories.* (pp. 367-408). Mahwah, NJ: Lawrence Erlbaum Associates.

Hanson, H. M. (1959). Effects of Discrimination-Training on Stimulus-Generalization. *Journal of Experimental Psychology, 58*, 321-334.

Harris, J. A. (2006). Elemental representations of stimuli in associative learning. *Psychological review, 113*, 584-605. doi:10.1037/0033-295x.113.3.584

Holland, P.C. (1990). Event representation in Pavlovian conditioning: Image and action. *Cognition, 37*, 105-131.

Honey, R. C. (1990). Stimulus generalization as a function of stimulus novelty and familiarity in rats. *Journal of Experimental Psychology: Animal Behavior Processes, 16*, 178-184.

Honey, R., & Bolhuis, J. J. (1997). Imprinting, conditioning, and within-event learning. *Quarterly Journal of Experimental Psychology, 50B*, 97-100.

Honey, R. C., & Hall, G. (1989). The acquired equivalence and distinctiveness of cues. *Journal of Experimental Psychology: Animal Behavior Processes, 15*, 338-346.

Honey, R. C., Horn, G., & Bateson, P. (1993). Perceptual-Learning during Filial Imprinting: Evidence from Transfer of Training Studies. *Quarterly Journal of Experimental Psychology Section B-Comparative and Physiological Psychology, 46*(3), 253-269.

Iordanova, M. D., & Honey, R. C. (2012). Generalization of contextual fear as a function of familiarity: the role of within- and between-context associations. Journal of Experimental Psychology: Animal Behavior Process, 38(3), 315-321. doi:10.1037/a0028689

Jones, P. M., Whitt, E. J., & Robinson, J. (2012). Excitotoxic perirhinal cortex lesions leave stimulus-specific habituation of suppression to lights intact. *Behavioural Brain Research, 229*, 365-371. doi:10.1016/j.bbr.2012.01.033

Kelley, K. (2007). Confidence Intervals for Standardized Effect Sizes: Theory, Application, and Implementation. *Journal of Statistical Software, 20*, 1-24.

Killcross, A. S., Kiernan, M. J., Dwer, D., & Westbrook, R. F. (1998). Effects of retention interval on latent inhibition and perceptual learning. *Quarterly Journal of Experimental Psychology, 51B*, 59-74.

Kruschke, J. K. (2013). Bayesian estimation supersedes the t test. *Journal of Experimental Psychology: General, 142*(2), 573-603. doi:10.1037/a0029146

Tzu-Ching E. Lin, Natasha M. Dumigan, Sergio A. Recio & R. C. Honey (2016). Mediated configural learning in rats, *The Quarterly Journal of Experimental Psychology*, DOI: 10.1080/17470218.2016.1188973

Lubow, R. E., & Moore, A. U. (1959). Latent inhibition: The effect of non-reinforced preexposure to the conditioned stimulus. *Journal of Comparative and Physiological Psychology, 52*, 415-419.

McLaren, I. P. L., & Mackintosh, N. J. (2002). Associative learning and elemental representation: II. Generalization and discrimination. *Animal Learning & Behavior, 30*, 177-200.

Müller, D., Gerber, B., Hellstern, F., Hammer, M., & Menzel, R. (2000). Sensory preconditioning in honeybess. *Journal of Experimental Biology, 203*, 1351-1364.

Olarte-Sanchez, C. M., Amin, E., Warburton, E. C., & Aggleton, J. P. (2015). Perirhinal cortex lesions impair tests of object recognition memory but spare novelty detection. *European Journal of Neuroscience, 42*, 3117-3127. doi:10.1111/ejn.13106

Pearce, J. M. (1987). A Model for Stimulus Generalization in Pavlovian Conditioning. *Psychological Review, 94*, 61-73.

Pearce, J. M. (1994). Similarity and discrimination: A selective review and a connectionist model. *Psychological Review, 101*, 587-607.

Rescorla, R. A. (1980). Simultaneous and Successive Associations in Sensory Preconditioning. *Journal of Experimental Psychology: Animal Behavior Processes, 6*, 207-216.

Rescorla, R. A., & Wagner, A. R. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning II: Current research and theory* (pp. 64-99). New York: Appleton-Century-Crofts.

Robinson, J., Sanderson, D. J., Aggleton, J. P., & Jenkins, T. A. (2009). Suppression to visual, auditory, and gustatory stimuli habituates normally in rats with excitotoxic lesions of the perirhinal cortex. *Behavioral Neuroscience, 123*, 1238-1250.

Robinson, J., Whitt, E. J., Horsley, R. R., & Jones, P. M. (2010). Familiarity-based stimulus generalization of conditioned suppression in rats is dependent on the perirhinal cortex. *Behavioural Neuroscience, 124*, 587-599. doi:10.1037/a0020900

Rouder, J. N., Speckman, P. L., Sun, D., Morey, R. D., & Iverson, G. (2009). Bayesian t tests for accepting and rejecting the null hypothesis. *Psychonomic Bulletin & Review, 16*(2), 225-237. doi:10.3758/pbr.16.2.225

Talk, A. C., Gandhi, C. C., & Matzel, L. D. (2002). Hippocampal function during behaviorally silent associative learning: Dissociation of memory storage and expression. *Hippocampus, 12*, 648-656. doi:10.1002/Hipo.10098

Tomsic, D., Berón de Astrada, M., Sztarker, J., & Maldonado, H. (2009). Behavioral and neuronal attributes of short- and long-term habituation in the crab *Chasmagnathus*. *Neurobiology of Learning and Memory, 92*, 176–182. doi:10.1016/j.nlm.2009.01.004

Vogel, E. H., & Wagner, A. R. (2005). Stimulus specificity in the habituation of the startle response in the rat. *Physiology & Behavior, 86*, 516-525.

Ward-Robinson, J., & Hall, G. (1996). Backward sensory preconditioning. *Journal of Experimental Psychology: Animal Behavior Processes, 22*, 395-404.

Ward-Robinson, J., & Hall, G. (1999). The role of mediated conditioning in acquired equivalence. *Quarterly Journal of Experimental Psychology B, 52B*, 335-350.

Whitt, E., Haselgrove, M., & Robinson, J. (2012). Indirect object recognition: Evidence for associative processes in recognition memory. *Journal of Experimental Psychology: Animal Behavior Processes*, *38*, 74-83.

Whitt, E., & Robinson, J. (2013). Improved spontaneous object recognition following spaced preexposure trials: evidence for an associative account of recognition memory. *Journal of experimental psychology. Animal Behavior Processes, 39*, 174-179. doi:10.1037/a0031344

Wynne, J. D., & Brogden, W. J. (1962). Effect upon sensory preconditioning of backward, forward, and trace preconditioning training. *Journal of Experimental Psychology, 64*, 422-423.

Xiang, J. Z., & Brown, M. W. (1999). Differential neuronal responsiveness in primate perirhinal cortex and hippocampal formation during performance of a conditional visual discrimination task. *European Journal of Neuroscience, 11*, 3715-3724.

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Work from Experiment 3 was performed as part of Emma Whitt's PhD thesis.

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Figure Captions

Figure 1.

Top: Experimental design of Experiment 1. C = 10 Hz clicker, T = 2-kHz tone, + = 0.5-s, 1.0-mA shock. During preexposure, rats in group CT received, separately and irregularly sequenced, non-reinforced preexposure to T and to C. Rats in group T received a similar preexposure treatment except that stimulus C was omitted. The two groups of rats received identical treatments during conditioning and test. During conditioning, rats received C+ pairings. During the test rats were presented with T. See text for complete details. Bottom: Mean instrumental response rates during T in the test of Experiment 1 expressed as responses per minute (RPM). Error bars indicate one standard error of their mean.

Figure 2.

Top: Experimental design of Experiment 2. C = 10 Hz clicker, T = 2-kHz tone, + = 0.5-s, 1.0-mA shock. During preexposure, rats in group CT received, separately and irregularly sequenced, non-reinforced preexposure to T and to C. Rats in the other three groups received a similar preexposure treatment except that either C, T or both C and T were omitted. The four groups of rats received identical treatments during conditioning and test. During conditioning, rats received C+ pairings. During the test rats were presented with T. See text for complete details. Bottom: Mean instrumental response rates during T in the test of Experiment 2 expressed as responses per minute (RPM). Error bars indicate one standard error of

their mean. The four groups' data are summarized on left and right panels as the two pairs of groups that are matched in their preexposure to the T.

Figure 3.

Top: Experimental design of Experiment 3. C = 10 Hz clicker, T = 2-kHz tone, + = 0.5-s, 1.0-mA shock. During preexposure, rats in group CT140, CT280, and CT420 received, separately and irregularly sequenced, non-reinforced preexposure to T and to C. The mean inter-trial interval differed in the three groups during preexposure. Rats in group T received a similar treatment but with the omission of C and group 0 received neither C nor T during preexposure. The five groups of rats received identical treatments during conditioning and test. During conditioning, rats received C+ pairings. During the test rats were presented with T. See text for complete details. Bottom: Mean instrumental response rates during T in the test of Experiment 3 expressed as responses per minute (RPM). Error bars indicate one standard error of their mean.

Group	Preexposure	Conditioning	Test
CT	C and T	C+	T
T	T	C+	T

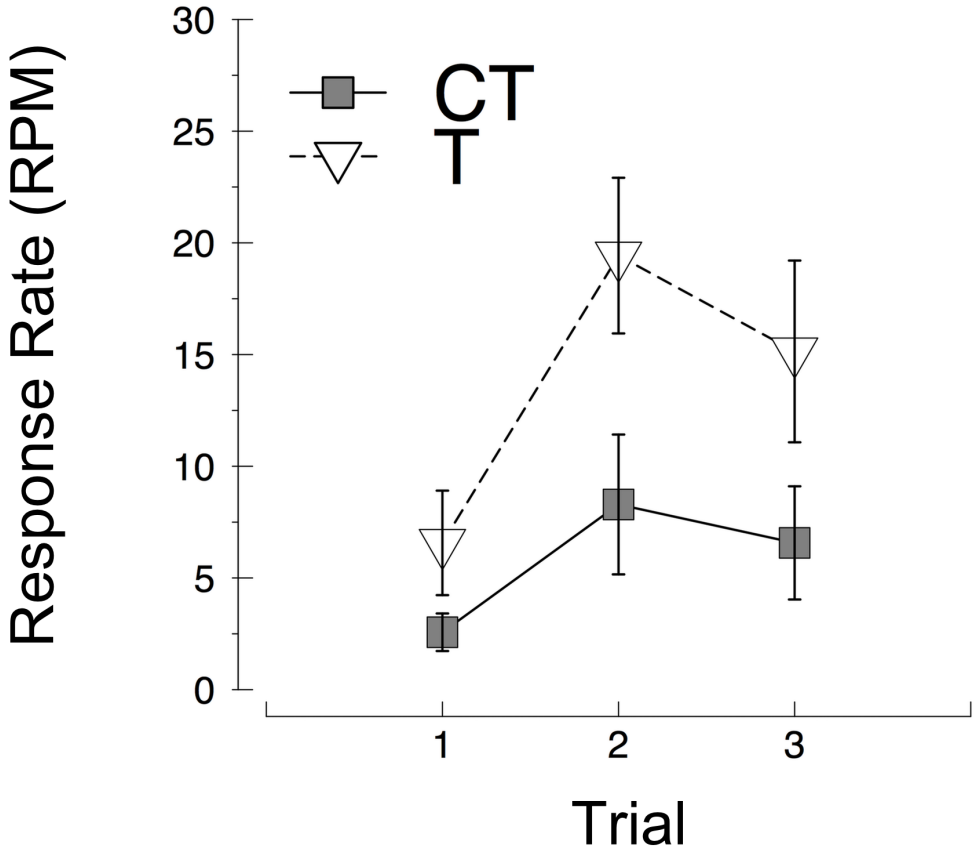

Figure 1

Group	Preexposure	Conditioning	Test
CT	C and T	C+	T
T	T	C+	T
C	C	C+	T
0	Nothing	C+	T

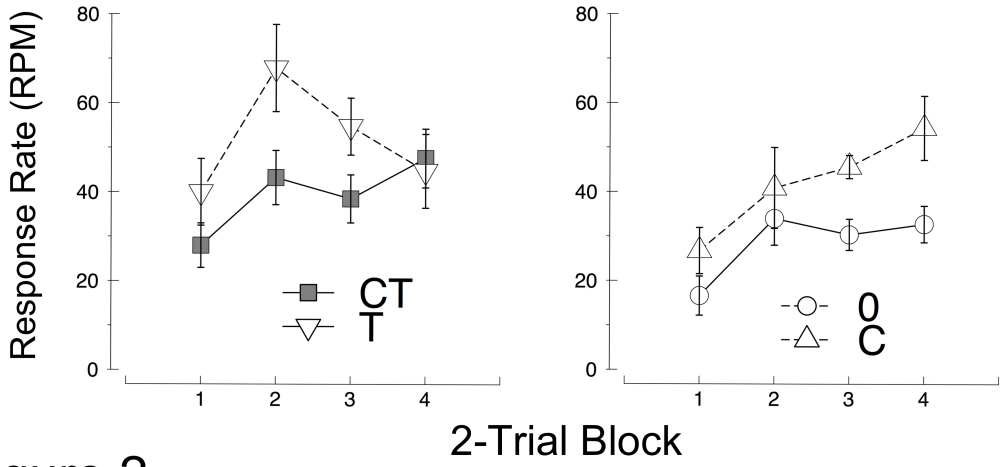

Figure 2

Group	Preexposure	Conditioning	Test
CT 420	C and T	C+	T
CT 280	C and T	C+	T
CT 140	C and T	C+	T
0	Nothing	C+	T
T	T	C+	T

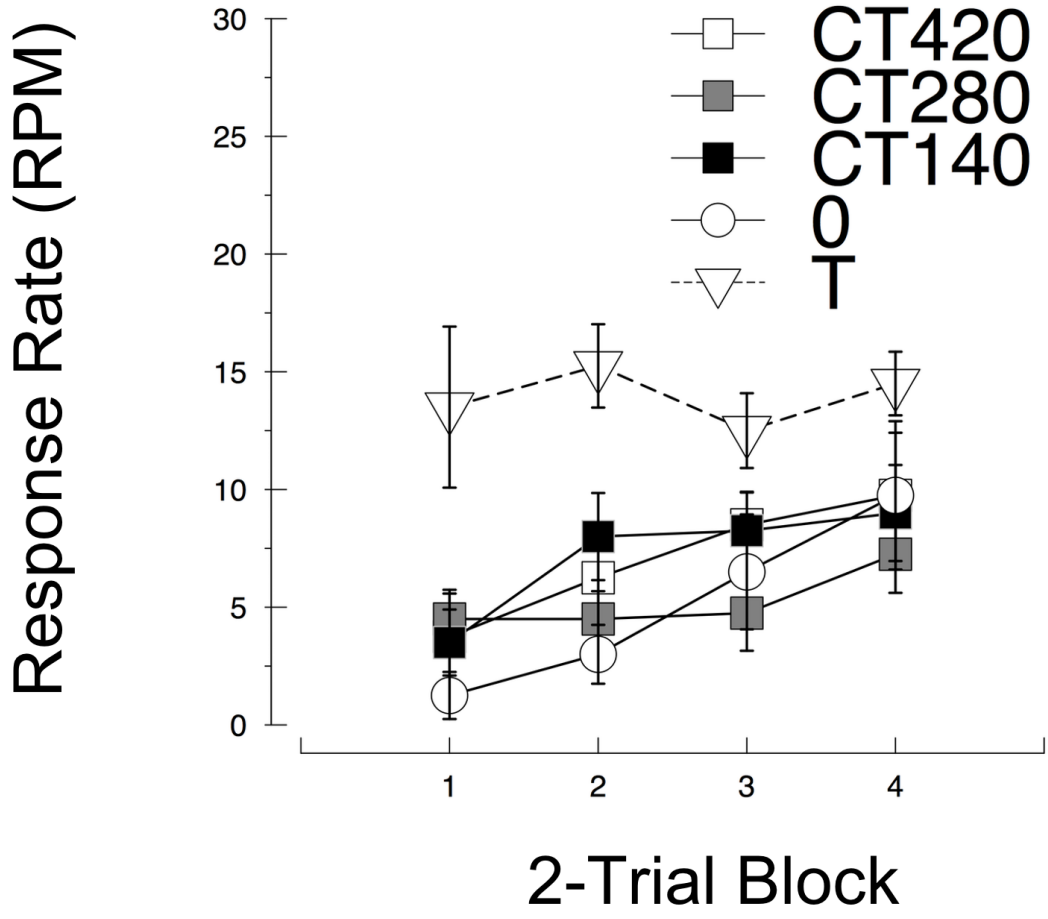

Figure 3

Table

Table 1

		C				T			
		Trial/Block							
Group	**Statistic**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**
					Experiment 1				
CT	Mean	8.0	15.1	11.1	22.6	6.0	10.9	9.7	11.1
T		-	-	-	-	4.6	8.6	6.9	11.4
CT	SEM	2.0	2.9	2.2	2.2	2.1	2.4	1.7	1.9
T		-	-	-	-	1.4	2.2	2.3	2.3
					Experiment 2				
CT	Mean	10.8	26.3	29.3	25.0	5.0	10.8	20.3	20.8
T		-	-	-	-	4.0	12.3	30.5	21.3
C		20.8	11.5	35.8	23.0	-	-	-	-
0		-	-	-	-	-	-	-	-
CT	SEM	3.5	3.9	5.0	3.3	1.3	2.4	3.4	2.4
T		-	-	-	-	1.4	2.5	6.5	3.6
C		4.8	2.9	5.3	3.4	-	-	-	-
0		-	-	-	-	-	-	-	-
					Experiment 3				
CT 420	Mean	2.3	8.3	10.3	12.3	7.5	12.3	11.3	10.0
CT 280		3.0	11.8	15.0	17.8	11.8	18.5	13.5	16.3
CT 140		0.5	7.5	13.5	13.8	6.3	15.0	11.3	12.5
0		-	-	-	-	-	-	-	-
T		-	-	-	-	6.0	8.8	14.3	13.0
CT 420	SEM	1.5	1.8	1.5	1.6	2.3	2.1	1.4	1.8
CT 280		1.8	2.8	2.3	2.0	2.3	1.7	1.6	2.3
CT 140		0.3	2.5	1.6	1.6	2.5	2.6	2.1	1.3

0	-	-	-	-	-	-	-	-
T	-	-	-	-	1.9	2.0	2.0	1.5

Note. Summary statistics for the response rates (responses per minute) during the first four trials, or two-trial blocks, of the pre-exposure stage of each of the three experiments. The leftmost and rightmost quartets of columns summarize responding to the clicker (C) and to the tone (T) respectively. "-" indicates that a group did not receive pre-exposure to either stimulus.

Table

Table 2

Group	Statistic	Trial/Block 1	2	3	4
			Experiment 1		
CT	Mean	8.3	8.0	3.1	-
T		8.9	14.0	4.9	-
CT	SEM	3.4	3.4	1.2	-
T		2.2	3.8	1.3	-
			Experiment 2		
CT	Mean	49.1	32.3	60.6	34.8
T		67.0	47.8	59.5	39.8
C		40.8	38.8	53.3	36.9
0		50.4	32.8	53.0	32.6
CT	SEM	4.9	3.3	6.8	3.1
T		7.0	5.9	8.1	4.2
C		7.0	4.2	7.0	4.7
0		9.5	2.5	4.3	4.9
			Experiment 3		
CT 420	Mean	11.0	9.5	10.8	8.0
CT 280		9.8	13.0	9.8	12.0
CT 140		11.8	13.0	11.3	10.3
0		12.0	13.0	11.5	8.3
T		9.5	9.8	15.5	12.3
CT 420	SEM	1.8	0.9	1.2	1.5
CT 280		2.2	2.6	2.5	2.3
CT 140		2.7	3.4	3.4	2.5
0		3.4	2.7	2.4	2.5
T		1.7	1.8	2.8	1.3

Note. Summary statistics for the response rates (responses per minute) during the 30-s period immediately preceding the test trials with the tone in each of the three experiments.

Group	Preexposure	Conditioning	Test
CT	C and T	C+	T
T	T	C+	T

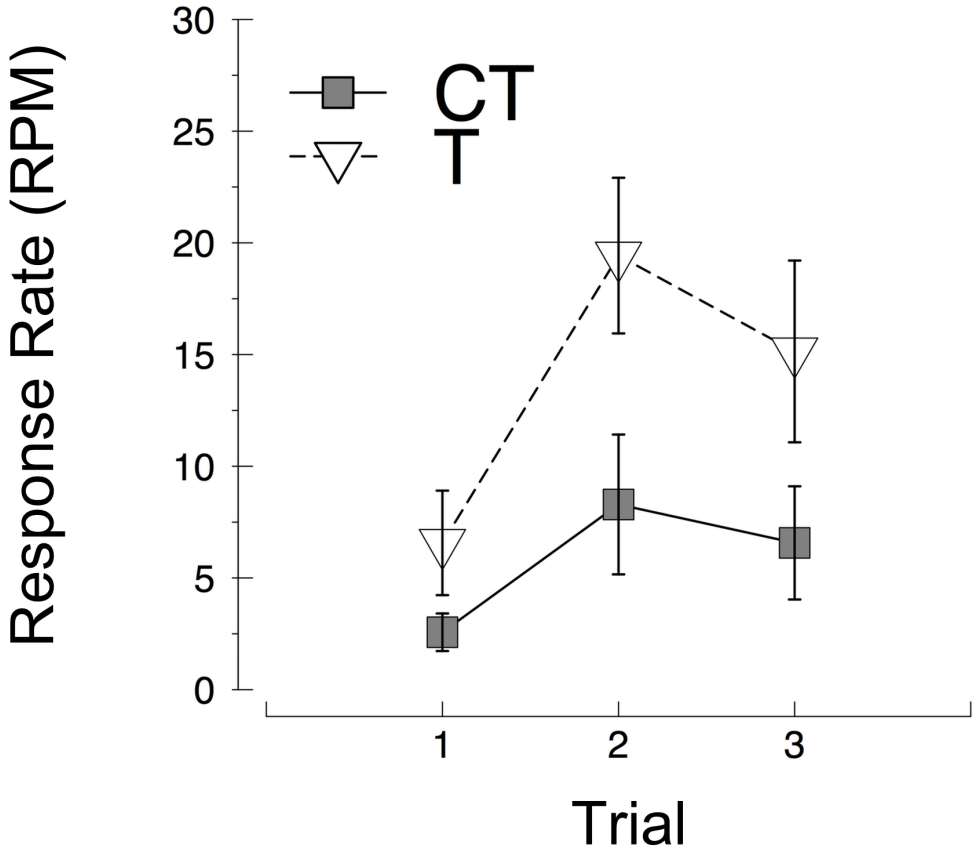

Figure 1

Figure

Group	Preexposure	Conditioning	Test
CT	C and T	C+	T
T	T	C+	T
C	C	C+	T
0	Nothing	C+	T

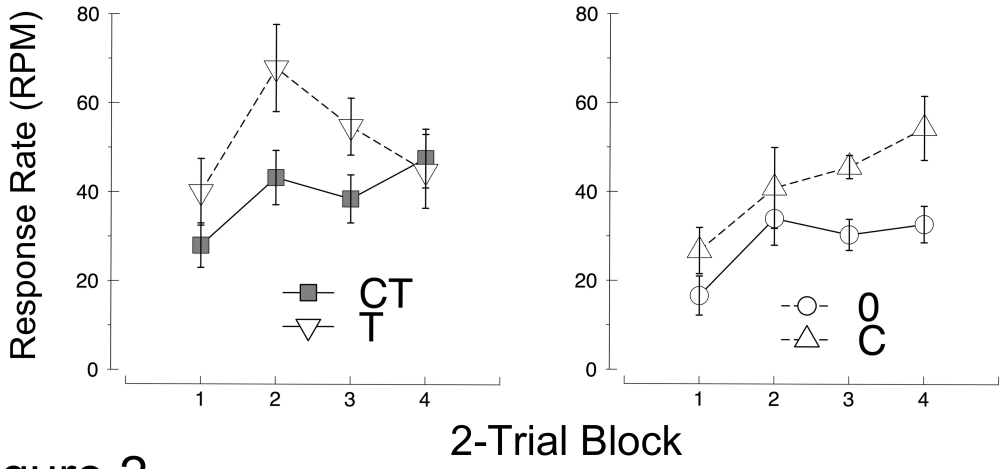

Figure 2

Figure

Group	Preexposure	Conditioning	Test
CT 420	C and T	C+	T
CT 280	C and T	C+	T
CT 140	C and T	C+	T
0	Nothing	C+	T
T	T	C+	T

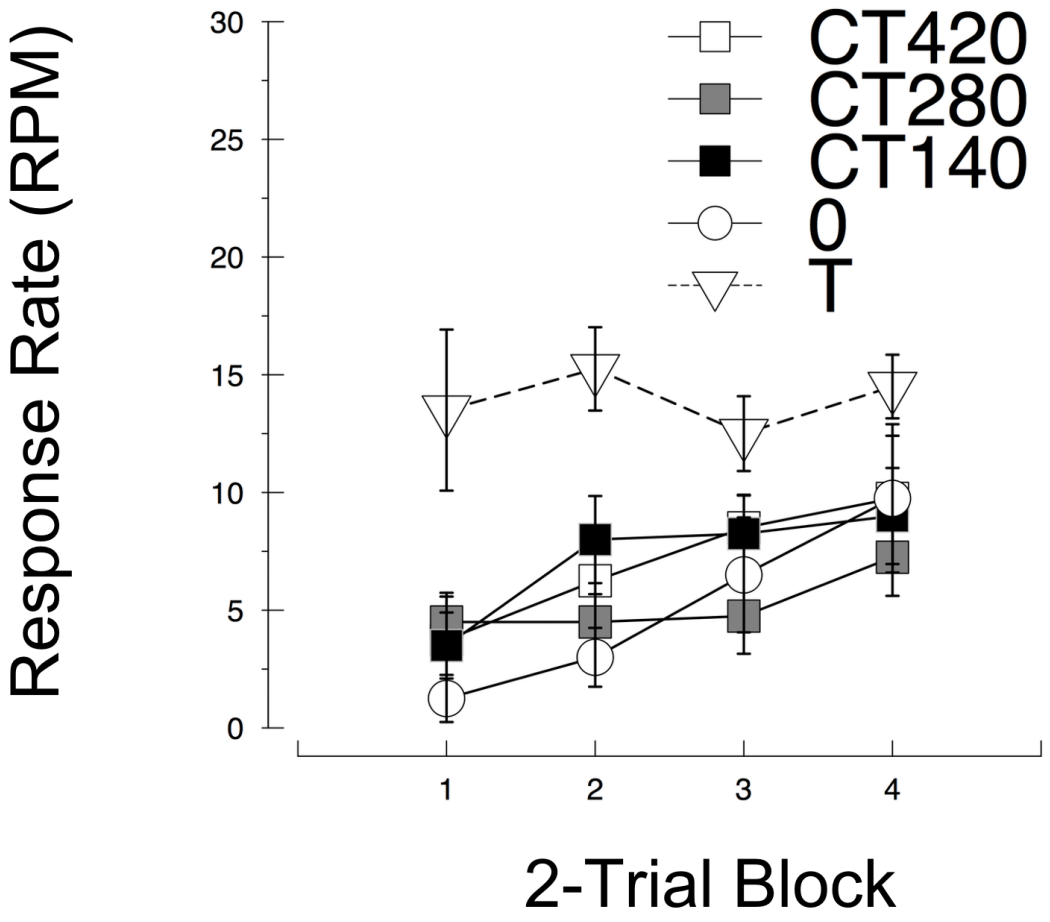

Figure 3